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Fragilariopsis kerguelensis size variability from the Indian subtropical Southern Ocean over the last 42 000 years

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Abstract: In the open Southern Ocean (SO), both modern and past size changes of the diatom *Fragilariopsis kerguelensis* appear to be strongly controlled by iron availability. Conversely, sea surface temperatures (SST) and sea ice seasonal dynamics take over in the seasonal sea-ice zone where iron is not limiting. No information exists on *F. kerguelensis* biometry from the subtropical SO, on the other extreme of the thermal and nutrient gradients. We present here new data on mean valve area of *F. kerguelensis* (FkergArea) from a sediment core covering the last ~42 cal kyrs from the southern Subtropical Front (SSTF) of the Indian sector of the SO, where iron and silica stocks are thought to have been consistently low over this period. Our results suggest that larger *F. kerguelensis* valves occurred during the Last Glacial period, and declined during the Holocene period. These findings indicate that more favourable SST, within the *F. kerguelensis* ecological range, during the Last Glacial period may have enabled *F. kerguelensis* to make better use of the low silica stocks prevailing in the subtropical zone leading to larger valves. Conversely, declining FkergArea during the deglacial and the Holocene periods may have been a result of higher SST which hampered the utilization of silica.

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Key words: biometry, diatoms, nutrient cycling, sea surface temperature

Introduction

Fragilariopsis kerguelensis (O'Meara) Hustedt is the most abundant diatom species in the surface sediments and in the down-core records of the open Southern Ocean (SO) (Zielinski & Gersonde 1997, Crosta *et al.* 2005a) and is believed to be a major silica carrier to the sea floor (Cortese & Gersonde 2008, Abelmann *et al.* 2015). *Fragilariopsis kerguelensis* size variability has recently been proved useful to infer recent (Cortese & Gersonde 2007) and past oceanic conditions at the glacial–interglacial timescales (Cortese *et al.* 2012, Shukla *et al.* 2013, Nair *et al.* 2015). A study conducted on sediment traps and surface sediments from the sea-ice zone to the subtropical zone of the Atlantic SO suggested a strong correlation of *F. kerguelensis* size with iron availability (Cortese & Gersonde 2007), consistent with the findings of culture experiments (Assmy *et al.* 2006, Timmermans & van der Wagt 2010) and *in situ* iron fertilization experiments (Assmy *et al.* 2007). Similarly, the down-core records from the Atlantic and Indian Antarctic Polar Front (APF), and Atlantic and Indian Sub-Antarctic Front (SAF) show larger *F. kerguelensis* mean valve area (FkergArea) throughout the last glacial period during higher aeolian dust flux to the SO. FkergArea generally declined during the deglacial and the Holocene periods along with a reduction in the dust flux (Cortese & Gersonde 2007, Cortese *et al.* 2012, Shukla *et al.* 2013). This pattern was reproducible until termination V, ~430 cal kyrs BP (Cortese *et al.* 2012). However, other sources of iron, such as iceberg surges, may have mediated larger FkergArea in the Atlantic SO during the last deglaciation, which explains the observed differences in temporal variations of the species mean size between the different SO basins (Shukla *et al.* 2013).

In addition to iron availability, sea surface temperature (SST) has been shown to play an important role on *F. kerguelensis* size, probably via the regulation of silica uptake, whereby diatoms seemed to grow larger initial cells at their optimal ecological range (Crosta 2009, Shukla *et al.* 2013). Indeed, SST sets the upper bound on SO diatom growth (Smith 1990). Furthermore, although higher SST increase the growth rate of *Pseudo-nitzschia multiseries* (Hasle) Hasle, a sub-Antarctic diatom related to *F. kerguelensis*, it also decreases cell size in this species (Boyd *et al.* 2016 and references therein).

Therefore, diatom size variation in the SO is controlled by both physical and biogeochemical components, and their non-linear interactions. Here, we present a 42 cal kyrs record of FkergArea from the Indian subtropical region of the SO, where the biogeochemical environment did not change much over this period (Crosta *et al.* 2005b, Beucher *et al.* 2007), to better understand the impact of SST on *F. kerguelensis* size variation and associated silica export.

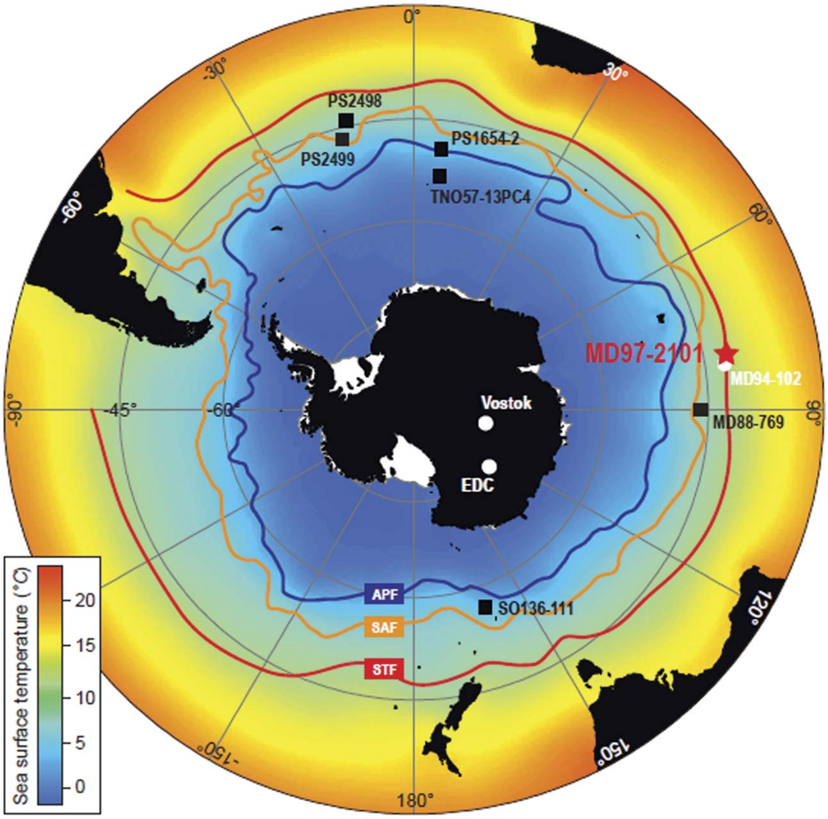

Fig. 1. Map showing the locations of the sediment and ice cores used in the study. Red star represents the MD97-2101 core from the Indian southern Subtropical Front for *F. kerguelensis* mean valve area (FkergArea) (present analysis) and the black squares represent previously published FkergArea records. White circles represent environmental records: core MD94-102 for the opal flux (Dézileau *et al.* 2003), and the Vostok and EPICA Dome C (EDC) ice cores for dust fluxes. The colour gradient represents the yearly average sea surface temperature (World Ocean Atlas 2009, https://www.nodc.noaa.gov, Locarnini *et al.* 2010). AFP = Antarctic Polar Front, SAF = sub-Antarctic Front, STF = Subtropical Front.

Materials and methods

The biometric measurements were performed on *F. kerguelensis* valves from sediment core MD97-2101 (43°30'S, 79°50'E, at the modern southern Subtropical Front (SSTF)) from the Indian sector of the SO (Fig. 1), retrieved during the Images III–IPHIS cruise on board RV *Marion Dufresne II*. The apical and transapical lengths were measured for 100 complete *F. kerguelensis* valves from each sample, for which the standard deviation was ~0.2 µm. Details on the measurements and calculations used in this study can be found in Shukla *et al.* (2013). To provide a direct comparison between all records, we recalculated published FkergArea records (Cortese & Gersonde 2007, Cortese *et al.* 2012) with the formula presented in Shukla *et al.* (2013). The age model of core MD97-2101, along with details on slide preparation, diatom counts and absolute abundance calculations are detailed in Crosta *et al.* (2005b).

To assess the role of *F. kerguelensis* in biogenic silica export to the sea floor (FkergBSi) in the Indian SSTF over the last 42 cal kyrs BP, and to provide a direct comparison with opal flux, we multiplied FkergArea by *F. kerguelensis* absolute abundance (FkergAbun), as has been performed for Antarctic and sub-Antarctic records (Shukla *et al.* 2013).

The down-core results and interpretations are described for three climatic periods namely the Last Glacial, the deglaciation and the Holocene which have been defined after Crosta *et al.* (2005b). The statistical analyses of FkergArea data with other data were performed using linear regression analysis and one-way ANOVA tests as detailed in Shukla *et al.* (2013). The down-core data for FkergArea, FkergAbun and FkergBSi are provided in Supplemental File A found at http://dx.doi.org/10.1017/S095410201600050X.

Results

The mean valve area of *F. kerguelensis* was largest during the Last Glacial period (~324 µm^2, $n = 24$), decreasing during the deglacial period (~296 µm^2, $n = 11$) and into the Holocene period (~275 µm^2, $n = 10$) (Fig. 2a green line). The results of the one-way ANOVA tests for FkergArea across the climatic periods are summarized in Supplemental File B found at http://dx.doi.org/10.1017/S095410201600050X. The FkergArea was statistically different between the Holocene and glacial periods, the Holocene and deglacial periods, and Last Glacial and deglacial periods ($P > 0.05$).

The absolute abundances of *F. kerguelensis* was highest during the glacial period (2.58×10^6 valves g^{-1}), especially during 41–35 cal ka BP (2.61×10^6 valves g^{-1}) and 20–17 cal ka BP (3.34×10^6 valves g^{-1}), and the Holocene

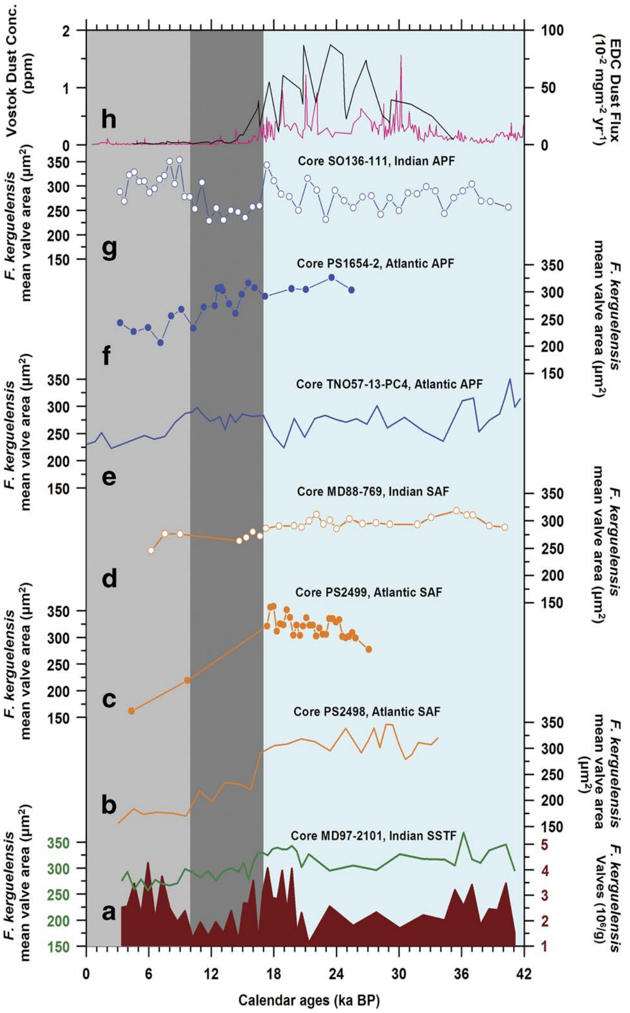

Fig. 2. Down-core records of **a.** *F. kerguelensis* mean valve area (green line) and absolute abundances (brown shading) in core MD97-2101 *vs* calendar age compared with previous biometric studies from the Southern Ocean: **b.** core PS-2498 and **c.** core PS-2499 from the Atlantic sub-Antarctic Front (SAF; Cortese *et al.* 2012), **d.** core MD88-769 from the Indian SAF (Shukla *et al.* 2013), **e.** core TNO57-13-PC4 from the Atlantic Antarctic Polar Front (APF; Shukla *et al.* 2013), **f.** core PS1654-2 from the Atlantic APF (Cortese & Gersonde 2007), and **g.** core SO136-111 from the Indian APF (Shukla *et al.* 2013). **h.** Dust flux record from EPICA Dome C (EDC) ice core (Lambert *et al.* 2008) (pink line) and dust concentration record from Vostok ice core (Petit *et al.* 1999) (black line), plotted on independent time scales; shown for direct comparison with *F. kerguelensis* mean valve area. The Last Glacial, deglacial and Holocene periods are highlighted with cyan, dark grey and light grey, respectively.

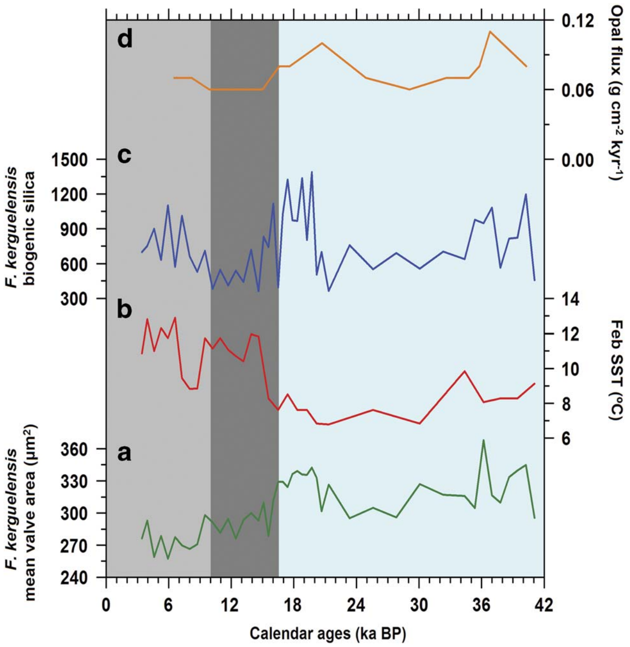

Fig. 3. Down-core records of **a.** *F. kerguelensis* mean valve area in core MD97-2101 *vs* calendar age (present study) compared with **b.** February sea surface temperature records of the same core (Crosta *et al.* 2005b). The reconstructed *F. kerguelensis* biogenic silica burial in **c.** is compared with the Opal flux record from the twin core MD94-102 in **d.** (Dézileau *et al.* 2003). The Last Glacial, deglacial and Holocene periods are highlighted with cyan, dark grey and light grey, respectively.

(2.78×10^6 valves g^{-1}). It was lowest during the deglacial period (1.99×10^6 valves g^{-1}) (Fig. 2a brown shading). The results of one-way ANOVA tests indicate that FkergAbun was statistically different between the Holocene and deglacial periods, and Last Glacial and deglacial periods ($P > 0.05$), but statistically similar for the Holocene and Last Glacial periods ($P < 0.05$) (for a summary of the one-way ANOVA tests see Supplemental File C found at http://doi.org/10.1017/S095410201600050X).

Finally, FkergArea data were compared with FkergAbun to infer the relationship between valve size and productivity. A positive linear relationship was found for the Last Glacial ($R = 0.31$, $n = 24$, $P = 0.02$) and deglacial periods ($R = 0.056$, $n = 11$, $P > 0.05$). While an inverse relationship was found for the Holocene period ($R = -0.58$, $n = 10$, $P > 0.05$) (for a detailed data set see Supplementary File D found at http://dx.doi.org/10.1017/S095410201600050X).

The reconstructed biogenic silica associated to *F. kerguelensis* burial was high during the Last Glacial period, especially during 41–35 cal ka BP and 20–17 cal ka BP, and during the late Holocene, and low during the deglacial and early Holocene periods (Fig. 3c).

Discussion

Previous studies have suggested that there are three main factors that control *F. kerguelensis* size variability, which are superimposed on productivity-dependent size reduction during asexual cell division. First, alleviation of iron deficiency in the open SO was shown to generate larger valves (Cortese & Gersonde 2007, Cortese *et al.* 2012, Shukla *et al.* 2013, Nair *et al.* 2015). Second, lengthening of the growing season induced by higher SST and early sea ice break-up may promote the production of longer initial cells in the seasonal sea-ice zone (Crosta 2009). Third, increasing SST may have a subordinate role to dust-bearing iron flux drop on *F. kerguelensis* size reduction over glacial terminations (Cortese *et al.* 2012). These findings demonstrate that the controls on *F. kerguelensis* size variability may change through space and time depending on the limiting factors and their interactions. Our new data on FkergArea from the Indian SSTF of the SO provide a northernmost end-member to published records and allow us to further explore the previous hypotheses.

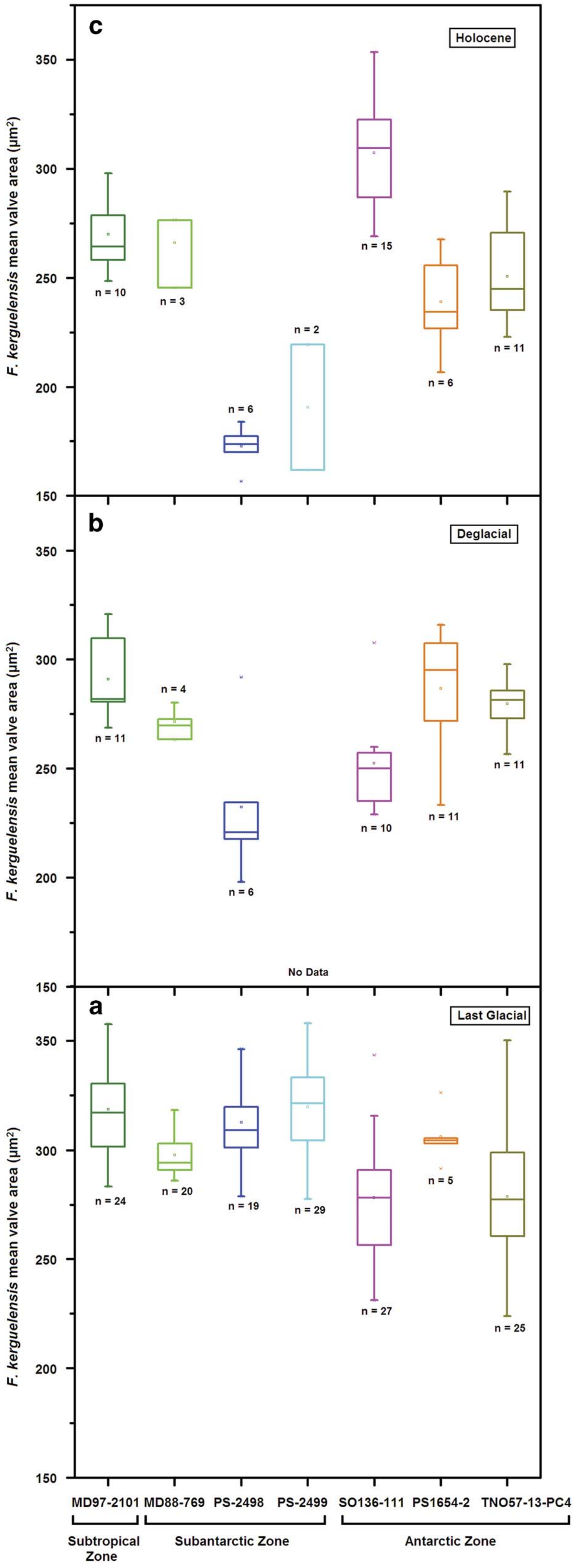

Fig. 4. Box and whisker plots showing variations in *F. kerguelensis* valve area for the **a.** Last Glacial, **b.** deglacial and **c.** Holocene periods for different cores in the Southern Ocean: core MD97-2101 (present study), cores PS-2498, PS-2499 and PS1654-2 (Cortese *et al.* 2012), and cores MD88-769, SO136-111 and TNO57-13-PC4 (Shukla *et al.* 2013).

Down-core records of F. kerguelensis *size in the Southern Ocean*

Our FkergArea record from the Indian SSTF (Fig. 2a green line) follow the general decreasing trend observed in previously published records (Fig. 2b–g). However, during the Last Glacial, FkergArea at the Indian SSTF site was larger than in the sub-Antarctic and Antarctic zones by 4–26 μm^2 and 18–45 μm^2, respectively (Fig. 4a). Likewise, during the deglacial period, FkergArea was larger at the Indian SSTF site than in the sub-Antarctic and the Antarctic zones by 25–64 μm^2 and 10–44 μm^2, respectively (Fig. 4b). During the Holocene, FkergArea at the Indian SSTF site was larger than in the sub-Antarctic Indian and Atlantic zones by ~9 μm^2 and 85–103 μm^2, respectively (Fig. 4c). The picture is more complicated for the Antarctic zone, where Indian SSTF FkergArea was larger than in the Atlantic sector core (by 24–36 μm^2; Fig. 2f) but smaller relative to the Indian APF sector core (by ~32 μm^2; Fig. 2g) where the largest FkergArea were found (Fig. 4c; Shukla *et al.* 2013).

Iron stress usually decreases diatom growth rate, silica maximal uptake rate and cell size (Leynaert *et al.* 2004, Timmermans *et al.* 2004, Timmermans & van der Wagt 2010). Conversely, it increases diatom silicification as a result of lengthening of the cell wall synthesis phase (Martin-Jézéquel *et al.* 2000). Therefore, the overall larger *F. kerguelensis* valves encountered in the warm, low-nutrient SSTF environment over the past 42 cal kyr BP probably resulted from low growth rates with fewer cell divisions, indicated by the very low absolute abundance in core MD97-2101 (Fig. 2a brown shading), which limited size reduction of the species communities.

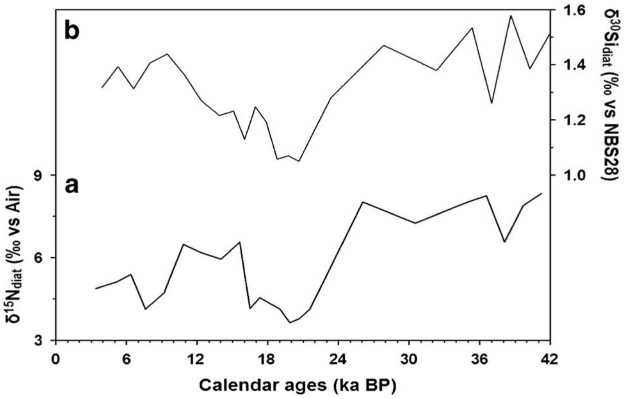

Fig. 5. Down-core records of **a.** $\delta^{15}N_{diat}$ data from Crosta *et al.* (2005b) and **b.** $\delta^{30}Si$ data from Beucher *et al.* (2007) for core MD97-2101.

Indeed, *F. kerguelensis* averaged ~2.5×10^6 valves g^{-1} in core MD97-2101 and between 20×10^6 and 180×10^6 valves g^{-1} in the other cores. The large FkergArea recorded during the Last Glacial period (Fig. 2b–g) may be a result of increased iron availability (Fig. 2h) (Cortese & Gersonde 2007, Cortese *et al.* 2012, Shukla *et al.* 2013). However, both data and models suggest that iron stocks in SSTF surface waters via dust, upwelling and sedimentary sources have been permanently low over the last 40 cal kyrs BP (Andersen *et al.* 1998, Lefèvre & Watson 1999, Mahowald *et al.* 2005, Lamy *et al.* 2014). Indeed, equivalence of isotopic composition of diatom-bound intrinsic matter $\delta^{15}N_{diat}$ and silicon stable isotopes $\delta^{30}Si$ data from the MD97-2101 core for the Last Glacial period suggested little impact of the iron supply on silicic acid and nitrate dynamics in the subtropical region of the SO (Beucher *et al.* 2007) (Fig. 5a & b). Therefore, we propose that other factors are responsible for the temporal variations in FkergArea recorded in core MD97-2101.

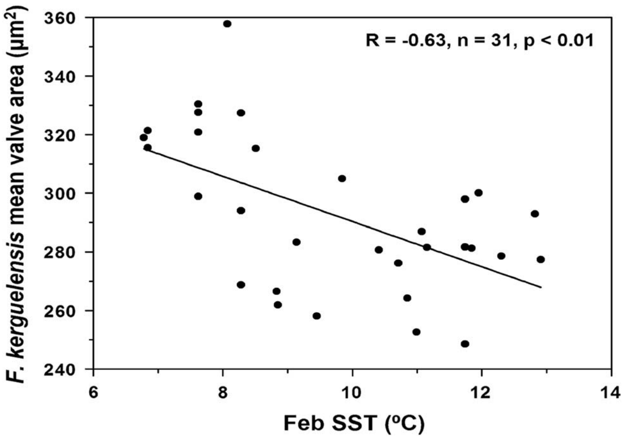

Fig. 6. Linear correlation between *F. kerguelensis* mean valve area and sea surface temperature in core MD97-2101.

Fragilariopsis kerguelensis *mean valve area and sea surface temperature*

The SST record at the Indian SSTF site presents a glacial–interglacial pattern (Crosta *et al.* 2005b) consistent with the global deglaciation. The SSTF FkergArea record appears inversely correlated to the SST record (Fig. 3a & b) materialized by a correlation coefficient of $R = -0.63$, $n = 31$, $P < 0.01$ (Fig. 6). Larger FkergArea occurred when SST ranged between 6–8°C during the Last Glacial period, while FkergArea started to decline during the deglacial period and continued into the Holocene period when SST increased by >8°C (Fig. 3a & b). FkergArea was smallest during the mid-Holocene period when SST was highest.

Maximum occurrences of *F. kerguelensis* in the phytoplankton occur between the winter sea ice limit and the SAF (Hasle 1969, Fenner *et al.* 1976, Froneman *et al.* 1995) and are similarly registered in underlying surface sediments (DeFelice & Wise 1981, Zielinski & Gersonde 1997). Preferential ecological conditions of *F. kerguelensis* generally fall within the 1–8°C SST range (Crosta *et al.* 2005a) where largest *F. kerguelensis* have been also observed (Cortese & Gersonde 2007). Conversely, smaller *F. kerguelensis* have been measured in surface sediments of the sub-Antarctic zone and the sea-ice zone where *F. kerguelensis* are less abundant. We propose that the occurrence of larger and more abundant *F. kerguelensis* at the Indian SSTF during the Last Glacial period (Fig. 3a) is a response to more favourable SST (6–8°C) (Fig. 3b). Conversely, a reduction in FkergArea

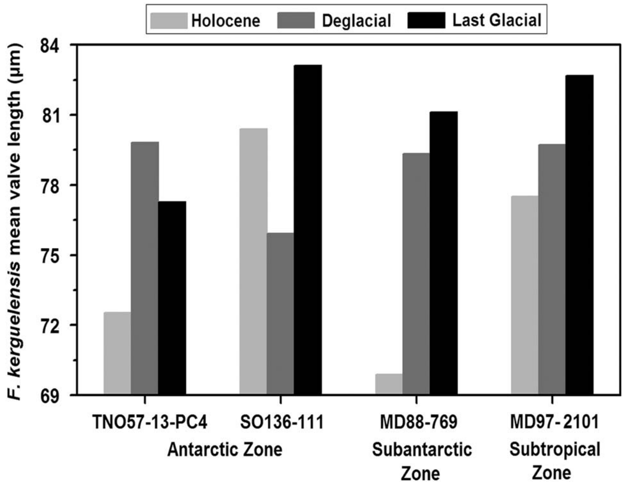

Fig. 7. *Fragilariopsis kerguelensis* maximum mean valve length variations for the Last Glacial, deglacial and the Holocene periods are shown for the different zones of the Southern Ocean: Antarctic zone (cores TNO57-13-PC4 and SO136-111; Shukla *et al.* 2013), sub-Antarctic zone (core MD88-769; Shukla *et al.* 2013) and subtropical zone (core MD97-2101; present study).

and FkergAbun during the deglacial period may have resulted from increasing SST > 8–9°C. The positive relationship between FkergArea and FkergAbun for 42–10 cal kyrs BP further supports that diatoms thriving at the adequate SST range grow larger initial cells (Fig. 7), supporting more numerous divisions, leading to larger communities. However, we found that the smallest *F. kerguelensis* co-occurred with highest abundances in the MD97-2101 core during the Holocene, at odds with the modern model (Cortese & Gersonde 2007). Although we do not have a definitive explanation for such a relationship change during the Holocene, we note that a recent study conducted on *P. multiseries* shows a twofold increase in growth rate, leading to decreasing cell sizes, when SST increases by 3°C (Boyd *et al.* 2016). Furthermore, small cells are believed to have a competitive advantage, through higher surface-to-volume ratios, under limiting nutrient conditions (Kiørboe 1993). Small cells also present higher growth rates, though slower rates of size reduction per generation, than larger cells (Amato *et al.* 2005, D'Alelio *et al.* 2009). We postulate that the co-occurrence of small but numerous *F. kerguelensis* during the Holocene may have resulted from the production of smaller initial cells (Fig. 7) for which rapid divisions could take place. The production of smaller *F. kerguelensis* may represent a specific adaptation to survive in the warm, low-nutrient, unfavourable conditions prevailing during this period (Fig. 2a).

Our observations suggest that SST changes dictated both *F. kerguelensis* productivity and size variations in the Indian subtropical zone over the last 42 cal kyrs probably via the mediation of silica uptake and the size of the initial cells. Indeed, studies on silicon metabolism suggest that efficient silicic acid uptake by diatoms can only be possible within the preferential environmental conditions of the species (Blank *et al.* 1986, Hildebrand 2000, Martin-Jézéquel *et al.* 2000). Our observations also extend, at the species level, previous findings demonstrating an inverse relationship between SST and phytoplankton community size (Hilligsøe *et al.* 2011).

Fragilariopsis kerguelensis represents the most abundant diatom in core MD97-2101, with relative abundances between 20–40% (data not shown). The good concordance between the estimated FkergBSi (Fig. 3c) and the opal flux (Fig. 3d) recorded in a twin core (Dézileau *et al.* 2003) suggests that this species is one of the main opal carriers to the sea floor in the subtropical Indian sector of the SO. However, despite a lower contribution to the diatom assemblages (10–20%), *Thalassiosira lentiginosa* (Janisch) Fryxell, a large heavily silicified centric diatom, was shown to export more biogenic silica at the Indian SSTF core site (MD97-2101) over the last 42 cal kyrs (Shukla *et al.* 2016). Similarly, *T. lentiginosa* was shown to be the main biogenic silica burial species to the sea floor in the open ocean sub-Antarctic and Antarctic zones (Shukla *et al.* 2016), although this species was never previously considered as such (Grigorov *et al.* 2002, Abelmann *et al.* 2006).

Conclusions

We investigated *F. kerguelensis* size variation over a 42 cal kyr period in core MD97-2101 from the Indian SSTF of the SO, where micro- and macronutrients are believed to have been consistently low. Our data provide a northernmost end-member to published records of diatom size variation and allow us to further explore the previous hypotheses. FkergArea was inversely correlated with SST over the last 42 000 years, with larger FkergArea during the Last Glacial period when SST were ~6–8°C declining during the last deglaciation into the Holocene period when SST increased by > 9°C. In contrast to other SO oceanographic realms where iron and nutrient concentrations strongly varied through time, our observations suggest that SST was the main factor controlling both the species' productivity and mean size in the subtropical zone, probably via the modulation of growth rates and silicic acid uptake. Further investigations on time series and sediment cores from the Indian and the other SO basins are required to refine the hypothesis proposed here.

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Author contributions

SKS and XC designed the project work. SKS generated the down-core biometry data. Both SKS and XC discussed the data. SKS wrote the manuscript and XC substantially contributed to manuscript writing.

Supplemental material

Supplemental files will be found at http://dx.doi.org/10.1017/S095410201600050X.

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